III. *On the Construction of Hexagonal Cells by Bees and Wasps.* By Frederick Smith, late Pres. Ent. Soc.

[Read 4th April, 1864.]

At the March meeting of this Society, Mr. Waterhouse propounded his theory of the construction of hexagonal cells by bees and wasps, and, supposing his to be the true solution of the problem, we are asked to accept it as explanatory of the manner in which all social insects form them. For years past I have had constant opportunities of examining nests of the social *Hymenoptera*, and I also formed a beautiful assortment of specimens for my own study; the result has been a conviction on my own part, that a different process obtains in different species; not that each particular species differs from all others, but that a variety of modes is observable amongst them in constructing hexagonal cells.

A mud-cell was exhibited to us by Mr. Waterhouse, and its mode of construction explained; whilst building this cell, the insect was stated to have always placed itself in one fixed position when at work, and the diameter of its cell was said to have been determined by the distance the insect could reach when thus at work. Now in that particular instance it no doubt was so; but had a hemispherical excavation of a similar diameter been made by a species of *Sphex*, by *Ammophila lutaria* for instance, that insect would have gone to work in a very different way. *Ammophila* is three times the size of the bee, but she would have moved round and round in different directions, until the same result was produced. Large insects frequently construct cells of smaller diameter than others built by smaller insects; and individuals of the same species may be observed at one time laboriously constructing cell after cell, whilst another is seen to avail itself of some ready-formed cavity, if equally adapted to its purposes. I am here alluding to solitary species; but I will show you this evening, that hive-bees will avail themselves of extraneous aid, and that if furnished with a series of pyramidal bases, they will readily erect hexagonal walls thereon; and I think you will see, that bees can form hexagonal-shaped cells without working in a circular direction at all, and

also without making circular excavations so close to each other as to necessitate the transformation into hexagonal cells, but which were intended to be cylindrical.

You were invited, at our last meeting, to arrive at the conclusion that all hexagonal cells were constructed in accordance with what is called the circular theory; that cell after cell arose from consecutively constructed hemispherical bases. An examination of a large number of nests has enabled me to ascertain that cells are constructed upon hemispherical, oval, pyramidal and also upon plane or flat bases. I have observed that cells are built upon bases consecutively formed, and also that the bases of entire combs are prepared before a single cell is constructed. Examples of each I shall lay before you, and having done so, I shall be much interested to have it shown, that all these various modes of building are in perfect accordance with the theory propounded to this Society at its last meeting.

Some writers upon the wonders of the hive have endeavoured to show that the hexagonal form of cell is, in some degree, necessitated for reasons that appear to me to have little weight. Saving of space is put forth as one! Surely not saving of space simply as such, without some collateral bearing, because the bees in a natural state are not constrained to occupy any particular-sized cavity. Then the saving of wax is supposed to operate, because wax is said to be a precious material secreted and elaborated in the stomach of the bee; and also in consequence of its being produced only by a certain class of working bees; but we must not lose sight of the fact, that hexagonal cells are not all built of wax; the scrapings of plants or of wood, used by many species of wasps, are not a scarce material; neither can mud, which is used by others, be said to be a precious or a rare material. Then as to the saving of labour, I cannot see that there is any better proof of this at all determining the desirability of the hexagonal-shaped cell; if honey-bees were left to their own resources, in localities to which they are indigenous, I believe that, like all other insects, they would just perform the amount of labour necessary to carry out the ends for which they are designed in nature; at the same time I see occasionally individuals of the same species, one labouring day by day in the construction of a nidus adapted to its purposes, whilst another avails itself of one ready made, but totally different in every respect to that formed by her laborious sister, but one that will answer her purpose; and in such instances I recognise a saving of labour. No, the hexagonal form of cell is the plan laid down by the

great Architect, and the bees are the builders that carry out His designs.

In the year 1858 this subject was brought before the Society by Mr. Tegetmeier, and at that time Mr. Waterhouse explained the nature of the circular theory, which, in his opinion, clearly elucidated the principle upon which all hexagonal cells are built by bees and wasps. My own observations on the mode of construction adopted by wasps, I found, in what was then assumed as essential to the formation of hexagonal cells, directly opposed, and I attempted, with such material as I at that time possessed, to combat the theory, which appeared to me inapplicable to the building of wasps; and I had the pleasure of finding, shortly afterwards, that one of our most intelligent inquirers held the same opinion.

Since that period Mr. Brown has advocated Mr. Waterhouse's theory in the "Zoologist," and the former gentleman assumes it as a fact, that no bee or wasp has been known to construct a single isolated hexagonal cell; contact with other cells, if I understand Mr. Brown rightly, being the essential condition which influences the hexagonal form; and if so, as regards complete cells, I take it for granted that it equally influences any portion of a cell that is raised into an isolated position; therefore I feel that I am warranted in assuming that no portion of a hexagonal cell can possibly be carried up above the surrounding cells, if the premises are infallible.

Mr. Brown gives it as his opinion, that "every cell during its progress is impinged upon by six other cells, and as all progress at the same time, the united attempts of the workers to avoid interspaces and to expend no more wax than is necessary to the making of firm walls, produce inevitably the hexagonal structure." Mr. Tegetmeier has given it as the result of his experience, "that the outer portion of each cell is cylindrical until a fresh cell is added on its outer side, when the cell becomes an inner one, and its outer sides transformed into a hexagon."

When this subject was last brought before the Society, I expressed my opinion to be, that the wasp commenced her comb with the intent instinctively to build hexagonal cells; since that time, I have had many opportunities of examining nests of wasps and bees, and the result is, if possible, a more confirmed belief in my original opinion. I shall have the pleasure of offering to your notice a number of most interesting examples of the architecture of wasps, and of pointing out the facts upon which my opinions are based; should I fail to prove my case to the satisfaction of a

single individual, I still think the exhibition of the different methods adopted by wasps in building their combs cannot fail to prove interesting.

It must not be supposed that all bees, or that all wasps, are equally skilful in constructing hexagonal cells; such is in fact far from being the case; some species, like unskilful masons, produce very unfinished or rustic work. This observation applies to wax-working bees, as well as to paper- and pasteboard-working wasps. The cells of *Trigona* are rude and unskilful in construction, when compared with the elegant and highly-finished structures erected by the hive-bee. Amongst the *Vespidæ*, the wasps belonging to the extensive genus *Polistes*, that construct cells of a papery consistency, are rude and unskilful in their work, when compared with those belonging to the genus *Chartergus*, which construct cells of stiff cardboard.

Wax is the material of which all honey-bees construct their cells; it is of a soft plastic nature, and is capable of being moulded, cut or scraped into any shape with ease; not so the pasteboard of wasps. The material of which the paper or cardboard is composed varies in different species; some use scrapings of sound timber, this is the case with the *Vespa Norvegica;* the nests of this wasp have a strength and durability adapting them for exposure to the vicissitudes of weather, being suspended to the branches of trees and shrubs; the hornet and other wasps, on the contrary, select decayed wood, consequently their nests are exceedingly fragile, and would soon perish if exposed. Many exotic wasps use materials of a vegetable nature, scrapings of the stems of plants; such is the material selected by pasteboard-working species; so firm and strong is the outer case, as well as the cells, of these wasps, that it is a difficult matter to tear them asunder. A few species build their pensile habitations entirely of clay, some nests being as much as eight or nine inches in diameter, and of an oblong, or egg-shaped, form; a specimen of an unfinished comb I shall lay before you.

We will now examine a little into the differences observable in the architecture of bees and wasps. Honey-bees, as you all know, build double combs, and these depend from the roof of the hive; the cells are consequently in a horizontal position. *Trigonæ* (stingless honey-bees) construct single combs; they are arranged horizontally, precisely like those of the common wasp, the mouths of the cells being consequently downwards; the combs, like those of the wasp, are supported by short columns of wax, or a material closely resembling wax, and of an equally soft

and ductile quality. Let me now direct your attention to the nests of various species of social wasps. The first which I will mention is the nest of *Icaria guttatipennis;* this is the nest to which I referred at a former meeting, as being figured in my Catalogue of the *Vespidæ*, and I incorrectly described it as being constructed of a single row of hexagonal cells; it consists of a double row, the number of cells being ten; I now direct your attention to the fact that all the cells are perfectly hexagonal, the exterior planes being as beautifully finished as those in contact with the inner planes of the opposing cells. I have placed a drawing of this nest (numbered 1) in the box on the table, and I particularly wish you to observe, that the first cell is carried up in a perfectly hexagonal form above the adjoining cells; a proof that, if wasps never build perfect isolated hexagonal cells, they certainly possess the capability of doing so. The exterior of all the cells, as I before observed, is hexagonal, not cylindrical until fresh cells are added on the outer side, as was observed to be the case in combs of the hive-bee by Mr. Tegetmeier. (See Pl. XIII. fig. B.)

I now invite observation to a nest, numbered 2, in the box of specimens; the portions exhibited are those of the exterior of a nest of *Nectarina Lecheguana*. The nest of this wasp is of globular shape, and is sometimes not less than sixteen or eighteen inches in diameter; the foundation is a single comb, inclosed in a globular envelope; *on this envelope* the wasps commence series of cells *on all sides;* these cells are covered in patches by envelopes,—the envelope always serving as the foundation of a fresh series of cells: a repetition of the above process, on all sides of the continually-increasing nest, results in structures such as I have described. Now you will observe, that all the cells constructed by these wasps are built upon the flat outer envelopes, and if you examine the specimens exhibited, you will see, in some instances, the faintest ground-plan of the hexagonal cell intended to be raised, traced on the flat foundation.

No. 4 is a portion of a nest of *Tatua morio*, perhaps the most interesting specimen that I offer to your notice; one that proves, to my mind, the primary intention of the wasp, instinctively to build cells with exactly six sides. *Tatua morio* is a pasteboard-maker; she constructs a bell-shaped nest, the outer envelope being very strong and tough; this would appear to be the first portion constructed, and next the flat floors upon which the cells are built; these floors are carried across the entire diameter of the nest, and attached to the outer envelope on all sides, each floor having a small circular opening left on one and the same

side, serving as a passage for the wasps from floor to floor, the entrance being at the bottom of the nest. I have sketched the section of one of these nests, and No. 4 in the box of specimens shows a portion of one of the floors, and also some unfinished cells. The nest sketched consists of nine chambers, all the floors are finished, but on the six upper ones only cells are constructed; a few are just commenced on the seventh. I have seen nests with cells on three floors only. In the nest sketched, the two lower floors are unoccupied, not a single cell having been commenced. In the box of specimens you will see one of these foundation floors without cells, and another upon which a number of the most beautiful hexagonal cells were in the course of construction. If the foundations of the planes of the exterior cells are examined, you will find one, two or more planes, clearly traced out as it were upon a ground-plan; if plans, so self-evident of intention, do not prove the instinctive purpose of the architect, I cannot imagine anything to my mind more perfectly conclusive. (See Pl. XIII. fig. D.)

It may not be known to some members of the Society, that in order to expedite the building of honey-combs, it is a common practice with bee-keepers in Germany to furnish hives with artificial foundations for the cells; these consist of sheets of wax, upon which is impressed a series of pyramidal hollows; in fact, the counterpart of a comb built by the bees themselves, entirely deprived of the cell-walls; and it is from such a piece of comb that the casts for the artificial foundations are obtained. A piece of casting of this description I lay before you, and I particularly call your attention to the commencement of the outer cells; you will see, in some instances, a single plane of the hexagonal cell commenced, in others two or three are in progress; here you have a ground-plan supplied, or, I may say, the foundations of the habitations ready prepared, upon which the labourers are to raise the walls, and you may see how admirably they have done it. Instinct enables the bee to construct hexagonal cells without teaching, and, we are told, in one undeviating manner. Surely the example before us exhibits an amount of intelligence on the part of the bees in availing themselves of such adventitious aid. Must we not henceforth, when speaking of the marvels of the hive or the vespiary, erase from our vocabulary such terms as blind instinct; and must we not cease to stigmatize the bee as a mere machine?

Before passing on to other considerations, let us here ask ourselves, what assumption naturally arises in the mind when we see,

as on the sheet of artificial bases exhibited, that the bees have at once availed themselves of this adventitious aid? does it not almost naturally occur to us, that these hexagonal ground-plans must be exactly such plans as they are accustomed to erect their hexagonal cells upon? does it not impress upon our minds the possibility, and even something more than that, the probability, that in whatever manner bees first commence their work, for instance, by making cylindrical excavations, does it not appear almost certain, that the bases of several cells are formed, and that each is perfectly pyramidal in shape, before a single wall is commenced? Such must be the conclusion arrived at by all who believe that insects can only work in one direction, and I think it must be admitted, that the very fact of the bees at once accepting the plan furnished, argues strongly in favour of the supposition that bees, when left entirely to their own resources, construct a precisely similar basement.

I would now direct attention to a large piece of a comb of the common wasp, *Vespa vulgaris*, and also to another of drone cells of the hive-bee, *Apis mellifica*, and I would point to a very marked difference in the construction of the cells; those of the hive-bee have always, whether finished or unfinished, a thickened rim of wax, the sides of the cells themselves are so thin and brittle that a constant traversing of the working bees over them would otherwise break and more or less destroy them. It is quite evident then, that whenever an addition is made to the height of a cell, this thickened rim must be scraped down to the same thinness as the planes of the hexagon beneath. This rim is always found on the cells, even when no further addition is intended to be made.

The wasp, you will observe, never requires a strengthening rim, the walls of her cells are carried up in hexagonal planes, to me, as evidently as if constructed by the hand of a mason.

Does then the fact of the bee always adopting the thickened rim indicate a different process of building, whereby the hexagonal-shaped cell is ultimately produced? or is it simply a necessity for insuring the safety of her work? Had it been removed when the cell was finished, I should have been led to suppose, that the cells of the hive bee were built by a different process; but, as it is always present, it rather appears to indicate the necessity of the rim as a mode of securing and strengthening the work.

So much, indeed, does the hexagonal principle appear to guide wasps in their operations, that one species, *Apoica pallida*, not only builds hexagonal cells, but she also, occasionally, constructs the entire comb itself of a hexagonal shape; now, here is no

compelling power, here are no adjoining circular combs, forcing the production of this particular hexagonal-shaped comb; the comb of this wasp consists of a single layer attached to trunks or branches of trees, &c., without any exterior envelope. I cannot, when I see such beautiful examples of the architecture of wasps, come to any other conclusion, than that, in instances such as the one I have just mentioned, it was the intention of the wasps to build hexagonal-shaped combs, and also their intention that those combs should consist entirely of hexagonal-shaped cells.

I direct your attention to a small nest of *Polistes tepidus;* this nest appears to illustrate, and to establish as a fact, a supposition that has frequently occurred to me, namely, that the development of the larvæ of *Hymenoptera* to the perfect condition must be a process much more rapidly carried on in tropical countries than in temperate ones, and that this rapidity of development necessitates the more rapid construction of those cells in which the first eggs are deposited. The nest before you, I think, is an exemplification of this idea: five cells are completed, each having served as the nursery of a wasp; twelve additional cells are commenced, and are in different stages of progress. Now I would call your attention to one fact, that the circumference of the unfinished cell is not carried up equally, or to the same height on all sides; you will observe that the two planes of each hexagonal cell that attach the unfinished cells to the finished ones are elevated obliquely considerably above the other planes; when any cell is carried up to the height required, all the planes have an equal elevation; therefore, it is clearly the case that the two inner planes that attached the unfinished cells to the finished ones must be first completed, leaving the two outer planes to be finished afterwards. This mode of construction is never, so far as my observation enables me to judge, to be observed in combs built by a populous community; in such cases, all the sides of the cells are carried up simultaneously.

I also exhibit a comb of the common wasp, *Vespa vulgaris* (No. 8), it is exceedingly interesting from the fact of its consisting of cells of different sizes; about three-fourths of the comb are occupied by cells of workers; at this stage of formation it became necessary to construct cells of a larger diameter adapted for females; this could not have been effected at once without a total disarrangement of their usual beautiful uniformity, but it could be done by degrees; thus we find the bases of about four rows of cells elongated, the parallel planes of the hexagons being also elongated, and thus by degrees the enlargement of the cells is

effected. The cells beyond the intermediate elongated ones will be found to be regular hexagons of the increased dimensions required. When I see such a departure from the usual mode of building as this, I recognize an intelligence that forces me to acknowledge in the wasp a creature that evidently designs an end to be accomplished, not a creature that would instinctively construct cylindrical cells, but whose labours always eventuate in the production of hexagonal ones, this result being dependent upon uncontrollable circumstances which always present themselves. (See Pl. XIII. fig. C.)

Five years ago, when the circular theory was brought before this Society, it did not appear in the same guise as now; it was then surrounded by certain collateral conditions, which I was led to believe were corner-stones of the ingenious edifice. Combination of labour was deemed essential, and at one period it was supposed that no solitary bee or wasp could construct hexagonal cells; this latter supposition proved to be a fallacy when I instanced the queen wasp as a solitary builder. In 1862, the Rev. Samuel Haughton, in a paper read before the Natural History Society of Dublin, says the hexagonal form of cell "may be accounted for simply by the mechanical pressure of the insects against each other during the formation of the cell. In consequence of the instinct that compels them to work with reference to a plane, and of the cylindrical form of the insects' bodies, the cells must be hexagons." This theory is, I think, at once disproved by the instance of the solitary wasp.

Another condition, essential (as I understood it) to the stability of the circular theory, was that no cell could possibly be constructed of the hexagonal form into which the builder could not insert its head. I exhibit the foundation comb of a wasp, and also the insect that constructed it (No. 6 in the box of specimens); I have taken off the head of the wasp and placed it over one of the cells, in order to show the impossibility of its being inserted.

The next condition that formerly existed was a circumstance that was supposed to regulate or determine the width of the planes of the hexagon; the explanation was this—a working bee was supposed to place itself exactly opposite the centre of one of the planes, and then fixing itself steadily in the proper position, the width of the plane would be the exact distance that the bee cut or reached with its mandibles when turning its head as upon a pivot. Now this at first sight appears a very ingenious solution; apparently it accounts admirably for the uniform exactitude observable in the width of all the planes; the uniformity of size in

the bees themselves also appears to add to the completeness of the theory; but it soon occurs to us that the same bees afterwards construct the larger cells of the drones. And we are no better off if we look into the nest of the wasp, for we find the large queen constructing the small cells of the workers, and the workers constructing the large cells of males and females.

I shall only mention one other position, still, I believe, upheld by the adherents to the circular theory; it is that no bee or wasp ever builds an isolated hexagonal cell, or a cell of hexagonal form carried up above the adjoining cells. If you examine the nest of *Icaria guttatipennis*, and also that of *Polistes Tasmaniensis*, both of which are exhibited, I think you will be satisfied that instances to the contrary are before you. I would also invite attention to a nest of *Vespa Norvegica* (No. 7), in which a central hexagonal cell is only raised to about one-third of its intended height, and has only four planes of the hexagon impinged upon by adjoining cells, the fifth and sixth cells not being commenced; this example will prove that the hexagonal form does not necessitate the impingement of six adjoining cells for its production, a position that has been laid down as being absolutely necessary.

No doubt it will be said that I have not shown the principle of the circular theory to be inapplicable to the construction of all hexagonal cells, but I contend that I have done so in several instances—in the nests of *Nectarina Lecheguana* and of *Tatua morio*, both wasps that erect hexagons upon flat bases; I have pointed out the fact that the commencements of single planes of the hexagon are to be found, in other cases of two or of three planes, and these beginnings exhibit not a trace of the circle any more than one, two, three or more pieces of masonry. I have shown that the bases of the cells of the common wasp, that constructs her cells upon consecutively formed bases, are hemispherical; in the hive we know they are pyramidal; and the bases of the transition cells, from those of the worker-wasp to those destined to contain females, partake more or less of the oval form.

Mr. Brown in his Essay remarks that "hive-bees produce their ordinary comb-cells by the united efforts of many individuals. Owing to this circumstance, and also to their never building up cells at the margins of combs unflanked by the foundations of other cells, they afford us, when so employed, no opportunity of observing the fundamental scheme upon which they build." My opinions are formed entirely upon observation of different modes of building; my conclusions have been forced upon me by facts,

in my opinion, conclusive of the primary intention of the builders to erect hexagonal cells.

I have examined nests of wasps in every stage of progress; I have found some species laying a separate foundation for each cell, wasps as well as bees; I have found some species of wasps constructing the entire foundations of a complete comb before a single wall of a cell was erected; and I see bees furnished with a complete floor of artificial foundations, at once adopting this adventitious aid. Then, again, I observe in nests of *Tatua morio*, and of some other species of wasps, the walls of one, two, three or more planes of the hexagon more or less raised; and, under these circumstances, what is the conclusion at which I naturally arrive? Why that all hexagonal cells are not constructed upon a circular principle, and that the primary idea of all social bees and wasps is not to produce cylindrical cells with hemispherical bases. I know not whether any one besides myself has arrived at a similar conclusion, or whether I stand alone in the opinion I have endeavoured to explain.

Addendum.—It having been suggested that the nest of *Icaria guttatipennis*, of which I could only exhibit a sketch, might possibly be only the portion of a nest in a state of demolition, I have re-examined it, and can vouch that such is not the case; only a few of the cells being carried up to their full height and lined with the *exuviæ* of the larva. It has also been stated that wasps are well known to destroy their old nests; such a circumstance is quite unknown to me, and I do not remember to have heard such a statement previously made.

In order to place clearly before my readers the fact of *Icaria* building hexagonal cells with exterior portions of the cells angulated, I have had a drawing of a nest of another species made, in which none of the cells are carried up to the required height. (See Pl. XIII. fig. A.) All the nests of this genus of wasp appear to be constructed in the same manner, the sharpness and beauty of the hexagon varying according to the skill of the particular species.

I exhibited a nest of *Polistes Tasmaniensis* in which a single cell was carried up above the surrounding cells, and it has been objected to as not being perfectly hexagonal: I have already stated that all bees and wasps are not equally skilful workmen, those belonging to the genus *Polistes* being instanced as "rude

and unskilful;" I admit that the elevated portion of the cell is not perfectly sharp and angular at the corners, but it is sufficiently so to prove the truth of my assertion. I recall attention to the cells of *Icaria*, which are exteriorly perfect in form, true hexagons, and I direct attention to the cells, particularly the exterior ones, in the figure of the nest of *Tatua morio;* it is to these I would point, and not to the least perfect example, as proofs of the fact of some species of wasps finishing the exterior portions of their cells in a perfectly hexagonal shape.—F. S., July, 1864.